SPECIES CROSSES IN HELIANTHUS: III. DELIMITATION OF "SECTIONS"[1]

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The genus *Helianthus* comprises 108 species, according to Watson (1929), although only about 70 would be recognized in a more conservative treatment. Asa Gray (1884) subdivided the genus into "annuals" and "perennials." It is perhaps significant that he failed to give Latin designations to his sections. Watson (1929) resorted to purely artificial groupings, the Rubri, in which the lobes of the disk corollas are red or purple, and the Flavi, in which the lobes are yellowish. The artificiality of this treatment is apparent when it is realized that several species are known in which both colors of disk corollas occur. However, it is true that the red and brown colors are common in the annuals and rather rare in the perennials. Rydberg (1932) in his treatment of 27 species for central North America set up six subdivisions, the annuals and five groups of perennials. Thus it is apparent that a completely satisfactory subgeneric classification, other than the recognition of annuals and perennials, has never been achieved for the genus.

In the first paper of this series (Heiser, Martin & Smith, 1962) it was pointed out that the genus comprised three more or less distinct groups: (1) North American annuals including the tap-rooted perennials, (2) North American herbaceous perennials, mostly from rhizomes, and (3) South American, more or less shrubby perennials. Although not all possible crosses have been attempted between the various species of the genus, a large number has now been made and a general picture of relationships, based on the results of hybridization, is beginning to emerge. It is now possible to divide the North American perennials group into two "sections": the "Divaricati," mostly confined to eastern and central North America, with the exception of *H. californicus* and *H. nuttallii*, and the "Ciliari," mostly limited to the southwestern United States and northern Mexico. Although for the most part the species of the two groups are well set off morphologically, as yet no completely satisfactory morphological characters have been found on which to base formal subgeneric classification. Additional study may reveal such characters, but it is entirely possible that none exist. It seems probable, nevertheless, that the four "sections," (1) the annuals and tap-rooted perennials, (2) the "Divaricati," (3) the "Ciliari," and (4) the South American perennials, form four distinct phylogenetic lines.

The present paper summarizes the results of artificial hybridizations not previously reported as well as certain other evidence bearing on the relationships of species. For descriptions of most of the species, reference may be made to Watson (1929). Herbarium specimens of the hybrids described here as well as their parental

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species, giving details as to source, are deposited in the herbarium of Indiana University. Table 1 gives a summary of the new hybrids and these will be discussed according to the headings listed therein.

"Annuals"

Hybrids between the species of the group are, with a few exceptions, readily secured and generally show highly reduced pollen and seed fertility. One of the most significant exceptions involves *H. agrestis* which thus far has not produced seeds in crosses with other annuals. Another kind of exception is seen with *H. tephrodes* (Heiser, 1955). This species is difficult to grow at Bloomington but a few hybrids have now been secured with *H. canus*. The high fertility of the hybrids and the fact that *H. tephrodes* is very similar to *H. canus* suggest that perhaps they had better be regarded as members of one species. The only hybrid secured in crosses of *H. tephrodes* with the apparently closely related *H. niveus* died as a seedling. Hybrids also have not been secured between *H. canus* and *H. niveus*, although they share many morphological features and both cross readily with *H. debilis* ssp. *debilis*.

The majority of the new hybrids involves *H. paradoxus*, a species recently described (Heiser, 1958) and earlier thought possibly to be extinct. Since the original description was based on a single specimen, several taxonomists (oral communications) questioned whether it was a "good" species. Therefore, I made a trip to the type area in 1961. Although I did not find the species at the type locality (7 miles west of Fort Stockton, Texas), I did find one population of about 50 plants ten miles north of Ft. Stockton *(Heiser 4779)*. The plants were growing in a moist, roadside meadow beside a stream, confirming the suspicion that this was more or less a paludose species. No other populations were found in spite of detailed search, although *H. annuus* was found to be extremely common in the area. It now seems probable that the natural hybrids of *H. paradoxus* previously reported (Heiser, 1958) probably involve *H. annuus* as the other parent rather than *H. neglectus*.

The plants were not yet in seed; but through the courtesy of Mr. Noel M. Hall, Jr., a local high school teacher, a large number of achenes were sent to me later in the year. Some of these were grown the following year at Bloomington and some at Urbana, Illinois, by Dr. Dale Smith. All 25 plants grown at Bloomington resembled the parent plants, but Dr. Smith reported that some of his plants were obviously hybrids with *H. annuus*. The plants collected in nature and those grown from seed fit the original description fairly well except that vigorous individuals may have a few prominent teeth in the lower part of the leaf margin and the stems are somewhat more harshly pubescent than those of the type. The chromosome number was determined as $n = 17$.

Reciprocal crosses of *H. paradoxus* with the annuals *H. agrestis*, *H. canus*, *H. niveus*, and the two perennials failed; but an abundance of seed was secured in crosses with five annual taxa. Those hybrids which were successfully grown all showed the highly reduced pollen stainability (Table 1) characteristic of the other

annual hybrids. Seed set varied from 0-20% in these hybrids upon open pollination, and controlled sister crosses gave no seed. The results of the hybridization and the fact that this species is quite distinct morphologically indicate that it is clearly entitled to the rank of species in spite of its apparently very restricted distribution.

"PERENNIALS: DIVARICATI"

All of the new hybrids in this group involve diploid species except the last (6347) which is between hexaploids. Three of the artificial hybrids now reported (6248, 6370, and 6371) confirm previously suspected natural or spontaneous garden hybrids (Heiser, Martin & Smith, 1962). The new hybrids are similar to those previously reported in this group in that few hybrid seeds are usually secured, but the hybrids show moderate to high fertility and exhibit a high number of bivalents at meiosis.

The hexaploid hybrid is of some interest since it marks the first successful cross with *H. californicus*. The species failed to give seeds in crosses to the hexaploids, *H. strumosus* and *H. tuberosus*, and several diploids. However, that *H. californicus* belongs to this group of perennials is supported by its morphology since it is very similar to certain forms of the diploid species, *H. nuttallii*, which readily crosses to other eastern perennial diploids. Although the hybrids of *H. resinosus* × *californicus* give very high pollen stainabilities (Table 1), seed set of sister crosses was low, ranging from 5 to 15%. The F_1 hybrids morphologically appear to be nearer *H. resinosus* than *H. californicus*. An F_2 generation, however, gave some segregates showing features of *H. californicus*. It is thus clear that the F_1's are true hybrids rather than selfs.

"PERENNIALS: CILIARI"

A group of species, *H. arizonicus*, *H. ciliaris*, *H. dissectifolius* and *H. laciniatus*, recently treated by Jackson (1963), morphologically form a very distinct group; and crosses of species within this group (*H. arizonicus* × *laciniatus* and *H. laciniatus* × *dissectifolius*) give rather fertile hybrids with a regular meiosis. To this group may be added *H. pumilus* of Colorado and Wyoming and *H. gracilentus* of southern California and northern Baja California, both diploids. Although morphologically somewhat removed from the remainder of the species of the group, these two species fit more nearly into this "section" than into any other. It is significant that hybrids of these have been secured in crosses to each other and with typical members of the group (*A. gracilentus* × *laciniatus* and *H. pumilus* × *laciniatus*, Table 1).

Helianthus cusickii, a diploid perennial of the northwestern United States, poses a somewhat special problem. Morphologically it is one of the most "extreme" species in the genus and does not clearly fit into any of the "sections." This species grows poorly at Bloomington and only a few crosses have been attempted with it. Crosses failed with three annual species and three eastern perennials but three weak plants were secured from a cross with *H. pumilus*.

That the perennials of this group are strongly isolated from the remainder of the genus is indicated by the crosses thus far attempted. Both the tetraploid and

hexaploid races of *H. ciliaris* have failed in crosses with three eastern tetraploid and three hexaploid perennials (Heiser & Smith, 1964). *Helianthus laciniatus* and *H. pumilus* have both failed to cross with three annuals and three eastern diploid perennials. Crosses have, however, been secured of *H. niveus* × *pumilus* and *H. niveus* × *laciniatus*, the former giving nearly sterile hybrids and the latter giving plants which died as seedlings (Table 1).

Annuals × Perennials

Although efforts have continued to secure additional hybrids between annuals and perennials using new strains of species previously tested, there are few new ones to report. Most of those that have been secured involve *H. niveus*, a species of Baja California; and it appears that this is the one species that bridges the North American groups as far as crosses are concerned. Hybrids of this species have also been secured with *Viguiera porteri* (Heiser, 1963). It is worth noting that Blake (1918) considered *H. niveus* as one of the two species intermediate betweeen *Helianthus* and *Viguiera*. In view of the hybridization results and that this species may be transitional to *Viguiera*, it is tempting to suggest that it is a "primitive" species which may be the nearest approach among living species to the original ancestral stock of *Helianthus*. Although placed with the annual group, it is a taprooted perennial; and such a species could have served as the progenitor of both the strict annuals and the perennials from rhizomes as was postulated by Babcock (1950) for *Crepis*.

The second new annual × perennial hybrid is *H. agrestis* × *floridanus*. The annual *H. agrestis* of Florida has failed to give seeds in crosses attempted with eight annual species and eight perennial species. There is some question regarding the taxonomic identity of the perennial parent (*Godfrey 62629*) although it is clearly closely related to *H. floridanus* and *H. angustifolius*. The hybrids secured were extremely weak and had malformed leaves and unusually small heads, and the flowers failed to produce anthers. Backcrosses attempted with the parental species as the male parents failed to produce seed. The failure of *H. agrestis* to cross with the other annuals raises some question about its placement in this "section." On morphological grounds it does not appear particularly closely related to the other annuals with the possible exception of *H. paradoxus* and at the same time it does not appear to be closely related to any perennial species.

In view of the fact that many of the annual × perennial hybrids have fairly good chromosome pairing, the statement made in the first paper of this series that there has been considerable differention in the chromosomes of the two groups requires some modification. However, the fact remains that all of the hybrids thus far secured are highly sterile which suggests that either genic or cryptic structural hybridity may be involved.

Hybrids of *H. annuus* with the perennials "*H. lactiflorus*, *H. maximiliani*, *H. rigidus*, and *H. scaberimus*" have recently been reported by Georgieva-Todorova (1960, 1962, 1963). Hybrids of both *H. rigidus* and *H.* × *laetiflorus* are not unexpected with *H. annuus*, since both of them are closely related to *H. tuberosus* which

is known to hybridize with *H. annuus*. It is difficult, however, to accept identifications of some of the perennials he has listed. His "*H. rigidus*" from the photograph given appears more nearly like *H. grosseserratus*. What he means by "*H. scaberimus*" since he cites no authority is uncertain. *Helianthus scaberrimus* Benth. is a synonym of *H. Bolanderi*, and *H. scaberrimus* Ell. is a synonym of H. *laetiflorus* (Watson, 1929). He gives no photograph of *H. maximiliani* but the "hybrids" insofar as can be determined from the photograph show no influence of that species. Furthermore, I cannot accept his suggestion that *H. maximiliani* and *H. annuus* are not very different genetically.

Pigment Analysis

In 1915 Cockerell found that the ligules of certain species of *Helianthus* when immersed in a KOH solution turned red to varying degrees whereas the ligules of other species showed no change. We have extended his observations to include all of the species which we have used in the crossing program reported in this series of papers except for *H. radula* which produces reduced ligules or lacks them entirely. For the most part at least three geographical samples have been tested for each species, and we have found that herbarium specimens give the same reaction as does living material although the intensity may vary to a degree. All members of the "western" and "eastern perennials" showed a positive reaction from moderate to strong, with the exception of *H. angustifolius* and *H. mollis*, which gave no reaction. Nine of the "annuals," on the other hand, gave negative results, while four species were positive. Of these last four, two, *H. anomalus* and *H. deserticola*, gave moderately strong reactions, whereas the other two, *H. agrestis* and *H. paradoxus*, gave very weak reactions. Thus, the reaction of KOH, probably indicative of a chalcone pigment, does not coincide exactly with the groups which have been set up as a result of hybridization and morphological studies.

Summary

Four "sections" may be recognized in *Helianthus*: (1) the annuals and taprooted perennials, (2) the "Divaricati," perennials primarily of central and eastern North America, (3) the "Ciliari," perennials, primarily southwestern North America, and (4) South American, more or less shrubby perennials. The "sections" are based primarily on the results of hybridization and it is thought that they may represent four different phylogenetic lines. Twenty-nine new artificial hybrid combinations are reported. Of particular interest among these are hybrids involving the recently described *H. paradoxus*. The results of the hybridizations along with morphological considerations indicate that this taxon justifies specific rank. Also of interest are the hybrids, *H. agrestis* × *floridanus* and *H. californicus* × *resinosus*, since they represent the first successful crosses involving *H. agrestis* and *H. californicus*. The possibility that *H. niveus* is "primitive" species is discussed. Reactions of ray flowers when treated with KOH do not give results that coincide with the "sections" as delimited above.

Table 1. New Artificial Interspecific Hybrids in *Helianthus*.

Accession Number	*Species*[1]	*Number of Plants*[2]	*Pollen Stainability Percentage*[3]	*Meiosis: Number of Bivalents*[4]
A. "Annuals"				
6041	argophyllus × neglectus	1	10	
6048	canus × tephrodes	4	99	
6318a	canus × debilis	3	25	15–17
6318b	debilis × canus	3	18	
6319a	debilis ssp. debilis × niveus	2	34, 88	(15–)17
6207	niveus × debilis ssp. debilis	4	64	15–17
	F_2 of above	4	86	
6320	niveus × debilis ssp. runyonii	2	5	15–17
6409	niveus × tephrodes	1; seedling died		
6325b	paradoxus × annuus (St. Louis)	7	8	9–11
6325c	paradoxus × annuus (Texas)	3	12	
6324b	paradoxus × argophyllus	4	6	13–14
6327b	paradoxus × debilis ssp. debilis	6	25	13–15
6328a	debilis ssp. runyonii × paradoxus	6	4	13
6328b	paradoxus × debilis ssp. runyonii	6	5	
6330	paradoxus × petiolaris	7	14	13
B. "Perennials: Divaricati"				
H579A	atrorubens × carnosus	2	49	
6414	atrorubens × floridanus	5	76	16–17
6248	decapetalus (2*n*) × carnosus	1	33	
H580B	heterophyllus × atrorubens	4	71	15–17
6371	longifolius × mollis	3	43	17
6371	maximiliani × decapetalus (2*n*)	7	84	17
6370	microcephalus × giganteus	6	55–97	17
H593B	mollis × decapetalus (2*n*)	3	82	17
6347	resinosus × californicus	5	98	quadrivalents present
C. "Perennials: Ciliari"				
6340a	arizonicus × laciniatus	4	91	17
H473a	cusickii × pumilus	3	30	17
H603a	gracilentus × pumilus	5	28	15–17
H603b	pumilus × gracilentus	1	15	
H585a	laciniatus × dissectifolius	3	79	
H585b	dissectifolius × laciniatus	6	93[5]	17
H586a	laciniatus × gracilentus	2	35, 63	
H586b	gracilentus × laciniatus	2	65, 85	13–15
H589	pumilus × laciniatus	1; seedling died		
D. Annuals × Perennials (including those mentioned in earlier papers*)				
*6199	canus × angustifolius	8	10	few pairs
*WM2014	debilis × floridanus	2	5	4–17
*H651B	debilis ssp. hirtus × occidentalis	2	4	?–17
6415	floridanus × agrestis	10	no pollen	
NIVJI	niveus × laciniatus	2; seedlings died		
*6374	niveus × microcephalus	6	10	14–17
*6211	niveus × nuttallii	2 (weak)	10	14–17
*6375	niveus × occidentalis	15	9	15–17
H644A	niveus × pumilus	1	13	13–17

[1] Female parent given first. Although all hybrids were made reciprocally, frequently only seeds from one combination germinated.

[2] In some cases a larger number of hybrids were secured in the annuals but only the number given was used for pollen counts.

[3] Mean given except in cases when there was considerable variability.

[4] Number of pairs observed in approximately 25 cells examined of one hybrid; where less than 17 pairs were observed the remainder of the chromosomes were associated in one or more chains or appeared as univalents.

[5] One plant showed 10%; the other five averaged 93%.

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